Zitteliana

An International Journal of Palaeontology and Geobiology

Series A/Reihe A
Mitteilungen der Bayerischen Staatssammlung
für Paläontologie und Geologie

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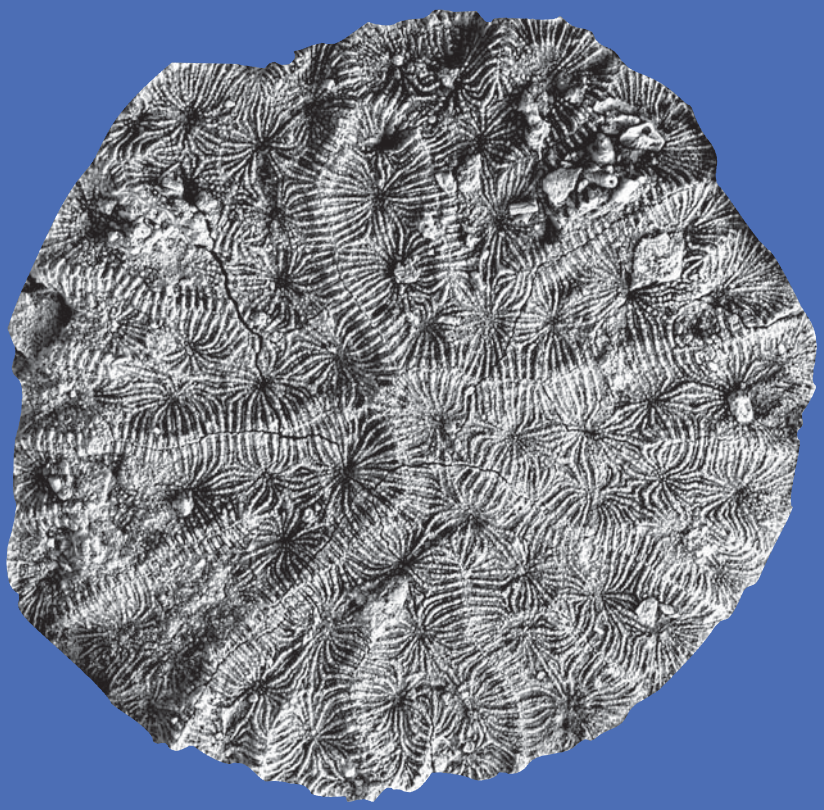

München 2006

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Bayerische Staatssammlung für Paläontologie und Geologie
Richard-Wagner-Str. 10, D-80333 München, Deutschland
http://www.palmuc.de/zitteliana
email: zitteliana@lrz.uni-muenchen.de

ISSN 1612-412X
Druck: Gebr. Geiselberger GmbH, Altötting

Cover Illustration: Coral *Collignonastraea meandra* (D´ORBIGNY, 1850) from the Toarcian (Lower Jurassic) of the Kuh-e-Shisui area (Iran); PIW2004III 40. For details see PANDEY & FÜRSICH: Jurassic corals from the Shemshak Formation of the Alborz Mountains, Iran, pp. 41-74 in this issue.

Umschlagbild: Koralle *Collignonastraea meandra* (D´ORBIGNY, 1850) aus dem Toarcium (Unterjura) der Gegend um Kuh-e-Shisui (Iran); PIW2004III 40. Für weitere Infomationen siehe PANDEY & FÜRSICH: Jurassic corals from the Shemshak Formation of the Alborz Mountains, Iran, S. 41–74 in diesem Heft.

Zitteliana	A46	75-83	3 Figs	München, 31.12.2006	ISSN 1612-412X

Palaeoclimatic implications of continental saline and fresh water mollusc communities of the Cenozoic Iberian Peninsula

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Manuscript received June 15, 2006; revision accepted September 10, 2006.

Abstract

Spatio-temporal distribution pattern of continental saline and fresh water mollusc palaeocommunities of the Cenozoic Iberian Peninsula were investigated in order to detect palaeoclimatic implications. Several thermophilous representatives of the Cerithioidea, which indicate a warm subtropical climate, are absent from the extant Iberian fauna and restricted to North Africa, the SE Mediterranean and Asia Minor. The fossil record suggests that the different continental aquatic ecosystems were colonised at different times in the Cenozoic: distribution pattern of *Melanoides* palaeocommunities (Oligocene, Ebro Basin; Miocene, Albacete; Pliocene, Barcelona; Lower Pleistocene, Guadix Baza Basin) and *Potamides* palaeocommunities (Oligocene Ebro Basin; Miocene, Duero Basin, Ebro Basin; Early Pleistocene, Guadix Baza Basin) and their successive disappearance since the mid- to Late Miocene in the northern Spain basins reflect the global Late Cenozoic temperature cooling. *Potamides* palaeocommunities in *playa lake*-environments of the Guadix Baza Basin indicate a semi-arid climate context, similar to the modern North African climate. Humid intervals are indicated by syntopic *Melanoides* palaeocommunities that colonised hyposaline environments, similar to the colonisation of aquatic ecosystems during the Holocene more humid climate episodes in North Africa. *Melanopsis* palaeocommunities are characterised by a greater temperature tolerance compared to the investigated *Melanoides* and *Potamides* palaeocommunities. The extant species *Melanopsis praemorsa* is distributed in Spain south of the 42nd degree of latitude, roughly coinciding with the +10°C-January-Isotherme, while the area of distribution of the Miocene congeners extended the northern Spain basin systems.

Key words: continental molluscs, Cenozoic, Spain, palaeoclimate

Kurzfassung

Zur Klärung paläoklimatologischer Implikationen wurden räumliche und zeitliche Verbreitungsmuster kontinentaler salinarer und Süßwasser-Molluskenvergesellschaftungen aus dem Känozoikum der Iberischen Halbinsel untersucht. Einige thermophile Vertreter der Cerithioidea, welche rezent nicht mehr auf der Iberischen Halbinsel vorkommen und heute in Nordafrika, dem südöstlichen Mittelmeer und Kleinasien verbreitet sind, zeigen warm subtropisches Klima an. Kontinentale aquatische Ökosysteme wurden zu unterschiedlichen Zeiten des Känozoikums von verschiedenen Vergesellschaftungen besiedelt: Verbreitungsmuster von *Melanoides*-Vergesellschaftungen (Oligozän, Ebro Becken; Miozän, Albacete; Pliozän, Barcelona; frühes Pleistozän, Guadix Baza Becken) und *Potamides*-Vergesellschaftungen (Oligozän, Ebro Becken; Miozän, Duero Becken, Ebro Becken; frühes Pleistozän, Guadix Baza Becken) und ihr sukzessiver Rückgang in den nordspanischen Becken seit dem mittleren bis späten Miozän spiegeln die globale spätkänozoische Temperaturabkühlung wieder. *Potamides*-Vergesellschaftungen in der *playa lake*-Fazies des Guadix Baza Beckens deuten auf ein semi-arides Klima hin, ähnlich dem heutigen Klima Nordafrikas. Phasen humideren Klimas werden durch syntope *Melanoides*-Vergesellschaftungen angezeigt, welche hyposalinare Ökosysteme besiedelten, ähnlich den aquatischen Ökosystemen zur Zeit der humideren Klimaepisoden im Holozän Nordafrikas. *Melanopsis*-Vergesellschaftungen sind im Vergleich zu *Melanoides*- und *Potamides*-Vergesellschaftungen durch höhere Temperaturtoleranz gekennzeichnet. Die rezente Art *Melanopsis praemorsa* kommt in Spanien südlich des 42. Breitengrades vor; eine Verbreitungsgrenze die etwa der +10°C-Januar-Isotherme entspricht. Das Verbreitungsgebiet kongenerischer miozäner Vertreter reichte dagegen über die nordspanischen Beckensysteme hinaus.

Schlüsselwörter: kontinentale Mollusken, Känozoikum, Spanien, Paläoklima

1. Introduction

The Cenozoic Iberian Peninsula has a rich continental sedimentary record, preserved in large depressions and smaller restricted basins, which predominantly formed after the Priabonian (Late Eocene) regression. The basin-systems arose

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induced by internal deformations of the Iberian micro-plate, coinciding with the formation of the Pyrenees and the Betic Orogene (Boccaletti et al. 1974; Hsü 1977; Riba et al. 1983; Puigdefábregas et al. 1986; Friend & Dabrio 1996). A wide variety of continental aquatic ecosystems and corresponding deposits established in these basins, which individual development was depending on the restriction of the basins or temporary or persisting connection with the Mediterranean Sea, palaeoclimate, local ground water hydrology and the geochemical composition of the sedimentary basement. Apart from perennial and temporary fresh water palaeoenvironments, athalasso-saline, i.e. continental saline ecosystems without marine connections, exhibited a broad spectrum of palaeohabitats for the colonisation by fresh water and saline mollusc palaeocommunities (Anadón 1989; Kowalke 2006a, 2006b); see also Beadle (1943), Williams (1981), and Hammer (1986) for general descriptions of the ecology of athalasso-saline ecosystems.

Fossiliferous deposits are particularly well known from the Ebro and Duero Basins (N, NW and Central Spain) and the Guadix-Baza Basin in S Spain (Fig. 1). The Ebro Basin formed along the southern margin of the Pyrenees. This large basin was characterised by two major marine transgressive episodes with subsequent regressions in the course of the Ilerdian-Cuisian (Early Eocene) and Lutetian-Priabonian (Middle to Late Eocene). Evaporitic accumulations, which have been deposited after the Pribonian regression, represent the terminal marine sedimentation. Oligocene and Neogene lacustrine fresh water and athalasso-saline sedimentary successions were subsequently deposited in the context of an intracontinental basin without marine connections (Bataller 1929; Riba et al. 1983; Anadón 1989). Similarly to the situation in the Ebro Basin, subsequent to the Priabonian regression Oligocene and predominantly Miocene successions were deposited in the Duero Basin, the south-western continuation, where the Neogene deposits discordantly overly the Palaeozoic and Mesozoic basement (Sánchez-Benavides et al. 1988, 1989). The northern margin of the Duero Basin is characterised by fossiliferous athalasso-saline and fresh water deposits of Miocene age, which are particularly well-exposed in the Burgos/Castrillo del Val area (Gonzáles-Delgado et al. 1986; Anadón 1989; Kowalke 2006b). The Guadix-Baza Basin represents an intra-montane depression, which is situated above the contact of the Betic and Subbetic Zone of the Betic Orogene. While Upper Miocene successions reflect a marginal marine palaeoenvironment with marine-brackish faunas, Pliocene-Lower Pleistocene deposits are characterised by alternations of fresh water and athalasso-saline faunas (Agustí et al. 1985; Anadón et al. 1986, 1987; Robles 1989; Kowalke 2006a, 2006b).

Apart from rather uncharacteristic basommatophoran fresh

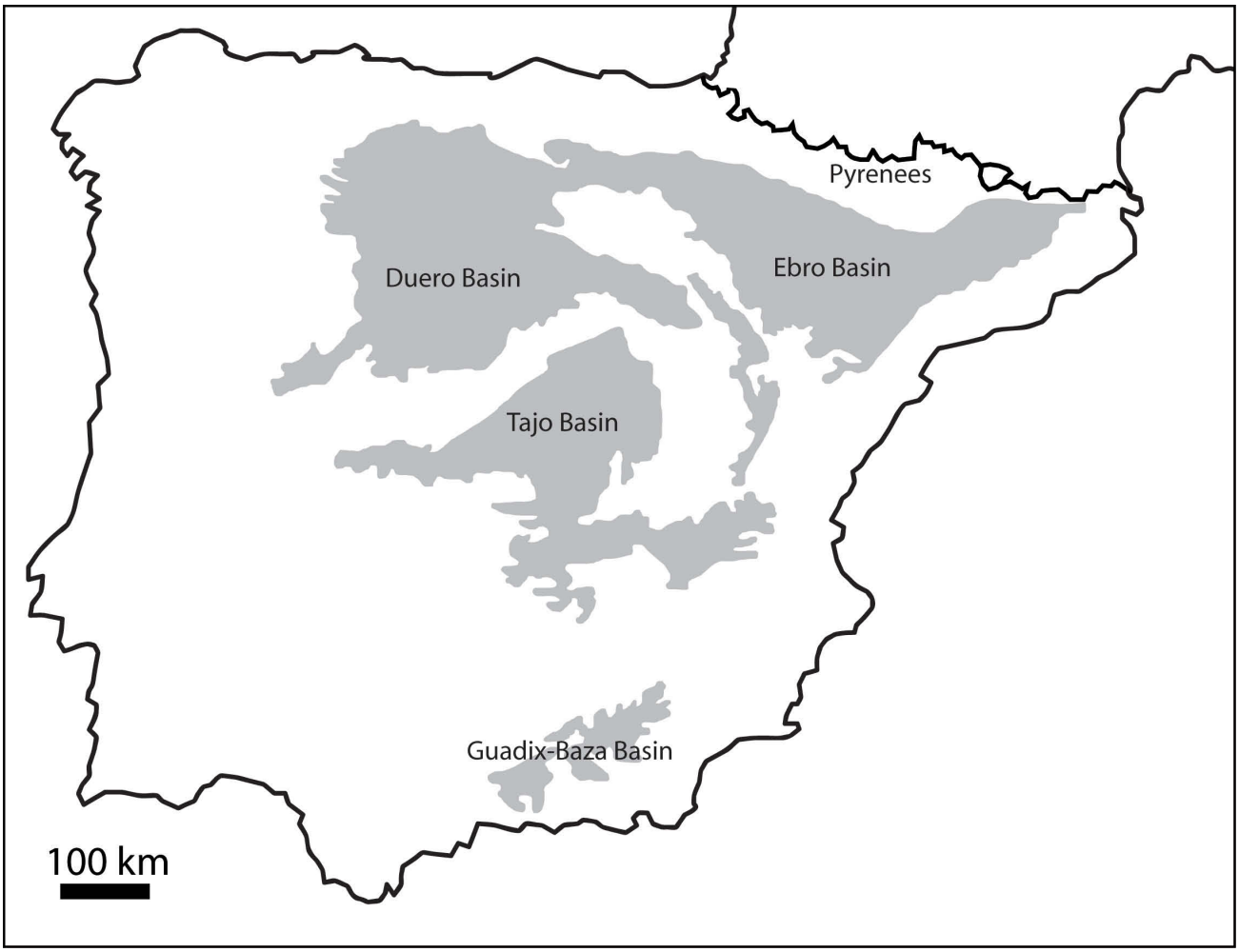

Figure 1: Location of the fossiliferous continental basin systems of the Iberian Peninsula.

water and archaeopulmonate paludinal faunas (Lymnaeidae-Planorbidae- and *Carychium*-palaeocommunities) with wide European distribution, several thermophilous fresh water associations (*Melanopsis*- and *Melanoides*-palaeocommunities) and athalasso-saline faunas (*Potamides-Corbicula*-, *Potamides-Cerastoderma*-, *Potamides-Hydrobia*-, and *Melanoides*-palaeocommunities) characterised the basin-systems in particular Cenozoic time intervals and were absent in others (Kowalke 2006b). The occurrences of these palaeocommunities may indicate time intervals during the Iberian history with considerably different distribution pattern of the characteristic faunas than present, probably reflecting different climatic conditions. Furthermore the presence of perennial aquatic ecosystems connected to riverine environments and the distribution of the corresponding palaeocommunities as well as sedimentological features may be indicative of precipitation rates different from the situation in the subhumid West Mediterranean climate zone of Iberia today (see e.g., Wallén 1970 for comparisons with the extant climate of the Iberian Peninsula).

The aim of the present study is to assess whether spatio-temporal distribution pattern of fresh water and athalasso-saline molluscs of Oligocene to Quaternary palaeoenvironments reflect the climatic development of the Iberian Peninsula. Comparisons with distribution patterns displayed by marginal marine Eocene faunas, contemporaneous faunas of the Mediterranean and Paratethys, and extant congeners have been carried out in order to document the mollusc faunal change and its palaeoclimatic significance.

2. The Tethyan precursors – evidence from Eocene euryhaline coastal palaeocommunities

Ilerdian and Cuisian (Lower Eocene) coastal sedimentary sequences of the southern Pyrenean Tremp-Graus Basin, which were deposited during the time interval encompassing the Early Eocene Climatic Optimum (EECO), are characterised by a rich record of mollusc associations. The coastal assemblages are composed of gradually changing mangrove/estuarine and shallow subtidal palaeocommunities (Dominici & Kowalke, in press).

The mangrove and estuarine palaeocommunities are composed of characteristic tropical caenogastropod genera, which are still dominating the mangrove ecosystems of the modern faunal bioprovinces: the Neotropis, the West African coast, the Western Indian Ocean and the Indo-Polynesian Province (van Regteren Altena 1942; Kowalke 2001; Plaziat et al. 2001). Several extant thermophilous genera of the families Cerithiidae (see Houbrick 1985; 1992), Potamididae (e.g., *Cerithidea* and *Tympanotonos*, cf. Houbrick 1984, 1991) and Thiaridae (*Melanoides*, cf. Brown 1980; Glaubrecht 1996), and extinct genera of Pachymelaniidae and Pachychilidae (see Kowalke 2001, 2004), which are morphologically very similar to their extant equivalents, document the tropical character of the faunas and the corresponding palaeoenvironments. Apart from these stenotherm elements, to lesser degree cerithioidean taxa such as *Granulolabium* formed part of the palaeocommunities (e.g., Lozouet 1986; Harzhauser & Kowalke 2001). These forms originated from the southern East Atlantic Province and exhibited a higher tolerance with regard to colder climatic conditions.

With regard to the faunal composition, the Pyrenean mollusc associations were very similar to the coastal faunas described from other European Eocene localities with tropical character, with several co-occurrences on genus level. For example, corresponding faunas are well-known from the Lutetian of SW France (Rouault 1848), the Paris Basin (Cossmann 1889, 1906a, 1906b) or W Hungary (Szöts 1953; Strausz 1966; Keckskeméti-Körmendi 1972; Kowalke 2001, 2004). Similar Tethyan coastal palaeocommunities, distinguished on genus level, have been described from South California, U.S.A. (Squires 1999).

Along with the decrease of the mangrove-ecosystems, coinciding with the climate cooling in the course of the latest Eocene/Early Oligocene (Plaziat et al. 2001), most of the associated molluscs such as *Cerithidea* became extinct in Europe and migrated in the direction of the tropical bioprovinces (Houbrick 1884; Harzhauser & Kowalke 2001; Kowalke 2003, 2005). A few coastal brackish water dwellers, e.g., *Granulolabium*, *Terebralia*, and *Tympanotonos*, exhibited tolerance with regard to decreasing temperatures and colonised the wet coastal ecosystems succeeding the mangrove palaeoenvironments (e.g., Moisescu 1969, 1972; Gitton et al. 1986, Plaziat et al. 2001).

Avicennia-dominated mangroves re-established during a temperature increase in the course of the Late Oligocene, with records in Spain, southern France and Hungary (Nagy & Kókay 1991) and probably far northward extensions to the Bavarian Molasse Sea (Barthelt 1989; Reichenbacher et al. 2004). The associated molluscs (predominantly *Tympanotonos* palaeocommunities) were restricted to the coastal brackish-marine ecosystems, since the mode of early ontogenetic development, i.e. the planktotrophic veliger phase, prevented the characteristic faunas from the colonisation of the continental saline ecosystems (Kowalke 2006b).

3. The continental uppermost Eocene and Oligocene record

The Oligocene Ebro Basin was characterised by extended palaeo-lake environments, which resulted in the deposition of thick successions of mudstones, limestones and coal series. Lacustrine deposits from the Lower Oligocene of Calaf within the eastern Ebro Basin consist of grey mudstones and intercalated layers of limestones, forming sequences which comprise up to one metre sediment. The marginal portions of this depositional environment are represented by marls rich in plant detritus and coal layers; see Cabrera & Saez (1987) for a detailed sedimentological reconstruction. The lacustrine ecosystem was characterised by an oligotypic freshwater fauna dominated by the thiarid *Melanoides albigensis* (Noulet), a species that is morphologically very similar to the modern type species *M. tuberculata* (Müller) (e.g., Brown 1980; Glaubrecht 1996; Kowalke 1998, 2006a). The accompanying fauna is rather uncharacteristic, being composed of fragmentary large pulmonates (*Lymnaea* sp.) and hydrobiids.

Melanoides represents a thermophilous element, which tolerates subtropical climates of N Africa and Asia Minor; for distribution data see e.g., Brown (1980) and Glaubrecht (1996). The extant type-species is pantropically distributed, but also occurs in North Africa and Asia Minor. Other extant thiarid genera are restricted to the tropics. While *Melanoides* represents a parthenogenetic direct developer which develops within a brood pouch, related thiarids need a fair connection of their habitats to the open sea, since they are characterised by a marine larval stage and enter the fresh water portions of rivers from estuarine habitats settled by juveniles after metamorphosis, subsequent to the planktotrophic development (Kowalke 1998).

The presence of palaeocommunities dominated by *Melanoides* indicates a warmer subtropical climate than extant. The perennial character of the faunas and the presence of extended fresh water ecosystems (cf. Cabrera & Saez 1987; Anadón 1989) reflect a considerably higher precipitation rate compared to the modern climate of the Iberian Peninsula, which belongs to the subhumid West Mediterranean climate zone (Wallén 1970). This climate zone is characterised by a mean annual precipitation rate of 400–800 mm, while the possible evaporation of 1000–2000 mm considerably exceeds this rate. The precipitation and evaporation rates in the Oligocene climate context of the Calaf-ecosystems should have been comparable in order to maintain in time an extended body of fresh water, see also Cabrera & Saez (1987) for a sedimentological-palaeohydrological interpretation.

Upper Oligocene athalasso-saline successions of the Ebro Basin are characterised by typical *Potamides-Corbicula* palaeocommunities, which are predominantly exposed in the plane of Zaragoza (Vidal & Deperet 1906; Bataller 1929; Anadón 1989) (Figs 2–3). The associations of perennial molluscs indicate the presence of persisting saline aquatic palaeoenvironments.

Apart from these ecosystems which reflect stronger, probably seasonal fresh water influx, during the Late Eocene common shallow saline lakes with characteristic micro-faunas existed in the Valldeperes region (Ebro Basin), composed of ostracods and foraminifers (Anadón 1978, 1989). The latter deposits lack a mollusc fauna, an absence that could indicate the temporary character of the water bodies in the context of temporarily and/or locally established semi-arid climate conditions inconvenient for the colonisation by a perennial mollusc fauna.

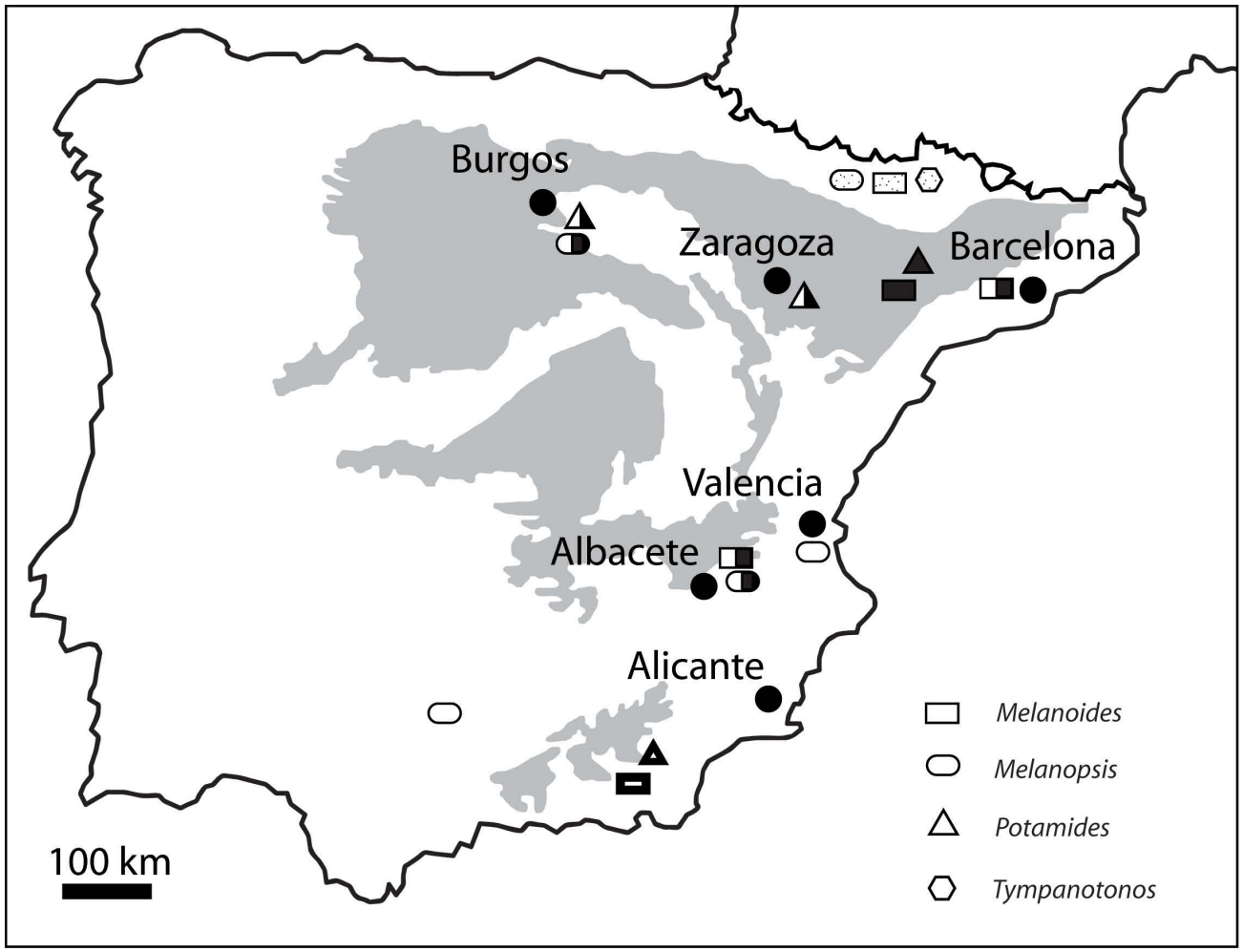

Figure 2: Occurrences of Iberian Cenozoic thermophilous gastropod genera. Dotted symbols indicate occurrences of Eocene coastal taxa; black symbols = Oligocene athalasso-saline taxa; half filled symbols = Miocene-Pliocene athalasso-saline taxa; black symbols with white centre = Lower Pleistocene athalasso-saline taxa; white symbols = extant occurrences of *Melanopsis*.

4. Evidence from Miocene athalasso-saline and fresh water faunas

While potamidid palaeocommunities dominated by *Tympanotonos*, *Terebralia* and *Granulolabium* and indicative of a warm subtropical climate, characterised marginal marine brackish to hypersaline environments with wide distribution in the Mediterranean and Paratethyan Upper Oligocene to mid-Miocene (e.g., Gitton et al. 1986; Lozouet et al. 2001; Harzhauser & Kowalke 2001, 2002; Harzhauser et al. 2002), corresponding assemblages are not found in athalasso-saline palaeo-ecosystems (Kowalke 2005, 2006a, 2006b). Oligotypic *Terebralia*-palaeocommunities were, for example, still present in the Upper Tortonian/Messinian partly hypersaline lagoon-systems with marine connections at Elche and Crevillente/Alicante, SE Spain (Kowalke 2006a). The accompanying fauna consisted of *Granulolabium*, *Cerithium* and juvenile bivalves of the genera *Cerastoderma* and *Abra*. Although *Terebralia* and *Granulolabium* were characterised by a wide Mediterranean Neogene distribution, they have neither been reported from fossil European athalasso-saline ecosystems (see e.g., Anadón 1989), nor from corresponding extant tropical environments (Kowalke 2005, and ecological data in Houbrick 1991). The entire spectrum of potamidids with planktotrophic larval development was hampered from the colonisation of continental saline ecosystems because larvae of gastropod could not sufficiently develop in stagnant water bodies (cf. Kowalke 1998, 2005, 2006a, 2006b).

Potamides represents the only known potamidid which lacked a planktotrophic larval stage and thus could colonise intracontinental saline lake-environments (Plaziat 1989, 1993). A characteristic palaeocommunity occurred in Upper Astaracian to Lower Vallesian (upper Middle to early Upper Miocene) athalasso-saline deposits of the Duero Basin (NW Spain) in the Castrillo del Val/Burgos area (Figs 2–3) where *Potamides gaudryi* Larrazet was associated with the hydrobiids *Hydrobia deydieri* Depéret & Sayn and *H. calderoni* Royo-Gomez. Apart from the saline fauna of marine origin, primarily freshwater but salinity-tolerant elements (see Reichenbacher et al. 2004; Kowalke & Reichenbacher 2005)

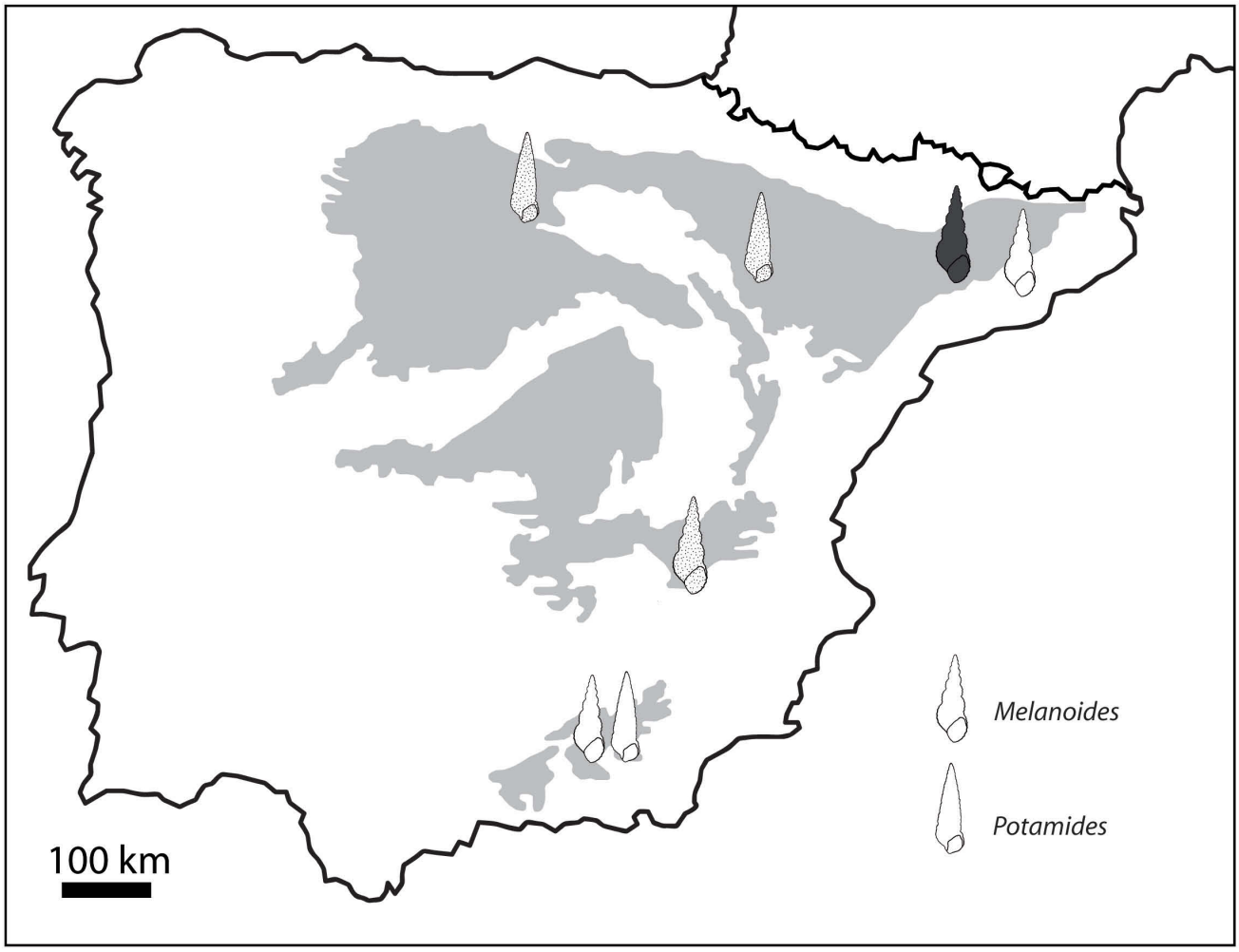

Figure 3: Spatio-temporal distribution pattern of the thermophilous genera *Melanoides* and *Potamides* in different continental facies and palaeoenvironments. *Melanoides*: black symbol = occurrence in Oligocene fresh water ecosystems; dotted = occurrence in Miocene fresh water ecosystems; white = occurrences in Pliocene and Early Pleistocene athalasso-saline ecosystems. *Potamides*: dotted = occurrences in Oligocene and Miocene athalasso-saline ecosystems; white = occurrence in Early Pleistocene *playa lake* ecosystems.

such as *Lymnaea* and *Theodoxus* formed part of the associations. These elements predominantly lived in small rivers or creeks which were connected with the athalasso-saline lake environment – an interpretation of the palaeo-habitat, which is also supported by sedimentological data. The euryhaline potamids established permanent populations that persisted for several years. This interpretation of the life-spans of individuals of *P. gaudryi* is probable, because the life-cyles of the closely related extant type species *P. conicus* (Blainville) from the South-East Meditteranean exceeded annual cycles and amounts several years (Kowalke 2003).

Associations similar to the palaeocommunities from the Duero Basin have also been documented from the Langhian and Serravallian of the Ebro Basin, particularly in the plane of Zaragoza (Muniesa, Belchite, Fuendetodos), where *Potamides* occurred in association with *Cerastoderma* (see Anadón 1989 and references therein).

The presence of the potamidid-dominated faunas in the Duero and Ebro basins during the Middle Miocene reflects a warm subtropical climate, since the closely related extant type-species *P. conicus* Blainville is restricted to the SE Mediterranean, distributed south of the 40th degree of latitude, along the N African coast and on the E Mediterranean Islands (Kowalke 2003). The persisting character of the palaeo-lake environments is – similarly to the situation during the Iberian Oligocene – indicative of a more humid climate compared to the extant climate of the Iberian Peninsula, with precipitation rates exceeding, or at most equalling the evaporation rates, and leading to the formation of extended riverine systems connected to the lacustrine palaeoenvironments with marginal swamps (Cabrera & Saez 1987).

Corresponding indications for the palaeoclimatic situation are also evident from Miocene fresh water faunas: extended Upper Miocene lacustrine habitats in SE Spain were colonised by characteristic thermophilous associations. For example, Mein et al. (1978) described freshwater deposits from the Turolian of Tolosa (NE Albacete) that are dominated by "*Melania*" (= *Melanoides*) associated with *Melanopsis*.

5. The Plio-Pleistocene fossil record and the extant distribution pattern

During the Late Messinian, the genus *Melanoides* inhabited hyposaline palaeoenvironments, which were previously colonised by *Potamides* spp. (Kowalke 2006b). The palaeocommunities are dominated by the species *Melanoides curvicosta* v. Martens, which is morphologically very similar to the modern type-species *M. tuberculata*. Apart from frequent occurrences of continental *Melanoides*-faunas in the typical Upper Messinian *Lago Mare*-facies of Italy (Esu & Girotti 1974; Esu 1980), similar hyposaline palaeocommunities have been described from athalasso-saline deposits from the Pliocene of Spain: *Melanoides tournoueri* (= *M. curvicosta*) occurred in a characteristic oligotypic association in Pliocene deposits of Barcelona, accompanied by *Neritina*, *Valvata*, *Melanopsis* and *Hydrobia* (Almera et al. 1892; Kowalke 2005).

In the course of the Early Pleistocene, the thermophilous element *Melanoides* was still characterised by a considerably more northern geographic distribution than extant. Anadón et al. (1987) and Robles (1989) reported probably hypohaline *M. tuberculata* associations from the Lower Pleistocene of the Guadix-Baza Basin. According to Esu (1980) contemporaneous faunas dominated by *Melanoides* occurred on the Balearic Islands. Extant natural populations of *M. tuberculata* are absent from the Iberian Peninsula (Álvarez-Halcón 1995). The species occurs in N Africa and Asia Minor (Brown 1980; Glaubrecht 1996; Kowalke 2005, 2006b). Artificially introduced Iberian populations of *M. tuberculata* are restricted to hydrothermal vents, e.g., the Alhama de Aragón/Zaragoza (see Álvarez-Halcón 1995).

Potamides-Hydrobia palaeocommunities characterised a shallow lacustrine *playa lake*- facies of the Lower Pleistocene Guadix-Baza Basin in the vicinity of Orce (Robles 1989; Kowalke 2006b) (Fig. 3). The occurrence of *Potamides* in playa-lakes is indicative of a warm subtropical semi-arid climate, comparable to the Holocene climate in N Africa. *Melanoides* faunas occurred well separated from the *Potamides* palaeocommunities in aquatic environments, which were characterised by lower salinity levels (Kowalke 2006b). The *Melanoides* associations could reflect episodes with at least seasonally higher precipitation rates and possibly subsequent exposure to progressive evaporation. Corresponding associations have been described from the Holocene of Algeria (Kowalke 2006b) and the Ethiopian Rift Valley (Leng et al. 1999).

The genus *Melanopsis* exhibited a higher tolerance with regard to the Late Cenozoic temperature decrease: *Melanopsis praemorsa* (Linnaeus) is still distributed in extant fluviatile environments of the Iberian Peninsula, occurring south of the 42nd degree of latitude. The northern limit of the area of distribution roughly coincides with the +10°C-January-Isotherme (see also Glaubrecht 1996 and Altaba 1998 for distribution data).

6. Climatic implications of mollusc faunal dynamics in other European continental sites

Corresponding climatically induced faunal successions and distribution patterns are rarely documented from European continental palaeoenvironments. The marginal marine-brackish Iberian fauna was not dissimilar to (Proto-)Mediterranean and Paratethyan Oligocene and Neogene *Granulolabium*-, *Terebralia*- and *Tympanotonos* palaeocommunities in being prevented from the colonisation of athalasso-saline palaeoenvironments by its indirect planktotrophic mode of early ontogenetic development (e.g., Harzhauser & Kowalke 2001, 2002, and references therein). *Potamides* represents the only potamidid which changed its predominant mode of indirect development to lecithotrophic and direct development and was thus able to colonise athalasso-saline habitats. Apart from the Neogene records in Spain, continental palaeocommunities dominated by *Potamides* have also been described from SW and central France (Rey 1965; Plaziat & Gaudant 1984).

Thermophilous *Melanoides* faunas are well known from the Middle Eocene of W Hungary, where they occurred in marginal fresh water environments adjacent to, but well separated from, the tropical Tethyan brackish coastal swamps (Kowalke 2001).

Melanoides assemblages are rarely documented from Upper Oligocene deposits of the Lower Brackishwater Molasse (Bavaria, S Germany) where the oligotypic fresh water palaeocommunities occurred well separated from the brackish *Tympanotonos-Polymesoda-* and *Granulolabium* associations (Reichenbacher et al. 2004) in a quiet water pond-facies (Kowalke submitted). Ottnangian/Karpatian and Badenian (Lower to lower Middle Miocene) brackish and fresh water deposits of the Upper Brackishwater Molasse and Upper Freshwater Molasse lack *Melanoides* faunas, although the palaeoenvironmental conditions would have been convenient (e.g., Kowalke & Reichenbacher 2005). The faunal composition of the palaeocommunities of the marginal Molasse Sea and subsequent fresh water palaeoenvironments point to a slight decrease in temperature, compared to the palaeoclimatological history of the Iberian Peninsula (Kowalke 2005, 2006b). However, the conditions still reflect warm climates, since *Melanopsis*, an element which exhibits a higher tolerance regarding slightly colder temperate conditions, was still present in Ottnangian deposits of the Bavarian Kirchberg Beds and the Oncophora Beds (Kowalke & Reichenbacher 2005). A stronger decline of the temperature is indicated by the composition of the Sandelzhausen fauna (Early Badenian, Bavaria, S Germany), which faunal composition lacks any thermophilous elements, and has apart from basommatophoran pulmonates even temperate to colder water elements, such as *Margaritifera* (Kowalke, own observation). A corresponding development could not be observed from the Iberian faunas, where *Melanoides* was present until the Early Pleistocene (Robles 1989; Kowalke 2006b).

Relic *Melanoides* palaeocommunities, which represented typical and ubiquitous associations of the Messinian *Lago Mare*-facies, have also been described from the Lower Pleistocene of southern Italy (Esu & Girotti 1974; Esu 1980).

7. Conclusions

Apart from the marginal marine-brackish mollusc associations and their spatio-temporal distribution pattern, the continental athalasso-saline and fresh water palaeocommunities provide evidence for the palaeoclimate of the Iberian Peninsula and its dynamic development in Cenozoic times.

Thermophilous potamidids and thiarids, which are today absent from the Iberian fauna and restricted to North Africa, the SE Mediterranean and Asia Minor, colonised various fossil continental aquatic ecosystems, which were characterised by different salinity levels: extended Oligocene to Upper Miocene fresh water and Plio-Pleistocene athalasso-saline palaeoenvironments were dominated by oligotypic *Melanoides* communities. *Melanoides* was characterised by a considerably more northern distribution than extant: occurrences within the Ebro Basin (Lower Oligocene) and NE Albacete (Upper Miocene) document a more humid and warmer climate than the extant climate of the subhumid West Mediterranean climate zone of the Iberian Peninsula, where precipitation and evaporation had comparable rates. Athalasso-saline *Melanoides*-faunas from Barcelona indicate a Pliocene temperature peak. Lower Pleistocene occurrences are restricted to the southern Spain Guadix Baza Basin. The lack of corresponding faunas in northern sites of the former area of distribution reflects the temperature cooling in the course of the Late Cenozoic.

The potamidid genus *Potamides* represents a second indicator of the Cenozoic climate development. *Potamides-Corbicula* associations frequently characterised Oligocene athalasso-saline deposits of the Ebro Basin. Miocene athalasso-saline ecosystems were characterised by oligotypic *Potamides-Hydrobia* (Duero Basin) and *Potamides-Cerastoderma* palaeocommunities (Ebro Basin). Similarly to the Pleistocene distribution pattern of the *Melanoides* palaeocommunites, *Potamides* was restricted to Andalusia during the Early Pleistocene, and was absent from the Iberian fauna since the Late Pleistocene. The Lower Pleistocene playa-lake environment, colonised by the *Potamides* palaeocommunities, indicates a semi-arid climate, similar to the modern North African climate. More humid intervals are indicated by hyposaline environments colonised by *Melanoides* palaeocommunities, comparable to Holocene humid-climate episodes recorded in North Africa.

Melanopsis faunas exhibit a greater temperature tolerance compared to the potamidid and thiarid associations. The extant melanopsid *M. praemorsa* is still present in fluviatile ecosystems of the Iberian Peninsula, distributed as far north as the 42nd degree of latitude, roughly coinciding with the +10°C-January-Isotherme, whereas fossil melanopsids were characterised by an area of distribution extending the basin systems of northern Spain.

Acknowledgements

Silvio Keller (Munich, Germany) assisted with the preparation of the figures. Michael Krings (Munich, Germany) improved the English. The paper benefited from the constructive review by Stefano Dominici (Florence, Italy). The Deutsche Forschungsgemeinschaft (DFG) financially supported my investigations of the evolution of brackish and inland saline molluscs (grant KO 2066/3-1). To all persons and institutions involved I express my sincere thanks.

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